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PARNASSIA AND SOME ALLIED GENERA

LULA PACE

(WITH PLATES XIV–XVII)

The systematists have had some trouble in classifying *Parnassia.* In an old Westphalian Flora by KARSCH (**15**) it is placed in the family Droseraceae. HALLIER (**12**), in discussing the Saxifragaceae, says *Parnassia* is much more closely related to the Droseraceae than to the Saxifragaceae; while EICHINGER (**6**) concludes that it should be placed with the Saxifragaceae as ENGLER (**8**) has it. WETTSTEIN (**26**) also places it there and takes Droseraceae out of the Sarraceniales and puts it with Parietales. The possibility of finding some characteristics that would help settle this question led to the present study. CHODAT (**3**) has used *Parnassia* to illustrate certain stages in the development of the embryo sac and embryo of angiosperms.

The work was undertaken at the suggestion of the late Professor STRASBURGER, and his continued advice was of the greatest service.

Parnassia palustris

MATERIAL.—The material which had been collected in Switzerland, and in the neighborhood of Bonn, Germany, was kindly placed at my disposal by Professor STRASBURGER. It had been killed in an alcohol acetic mixture (three parts of alcohol to one part of glacial acetic acid). The usual methods were followed in preparing the material for cutting. The younger stages were cut 5–6 μ thick and the older 8–10 μ. The triple stain, safranin-gentian violet-orange G, was most satisfactory, but iron-alum hematoxylin alone and with Congo red was also used.

The parts studied showed very few irregularities, or so-called abnormalities. Out of several hundred ovaries sectioned, the majority had five placentae, a few had four, two had three, and one had only two; in the last the two placentae were not quite normal in appearance. One ovary had a very irregular structure; it was as if the carpels had not grown together, and more or less perfect anthers, containing apparently normal pollen, were found on these (fig. 70). One anther had developed on a staminodium; two anthers were normal in appearance. CHAMBERLAIN (**2**) has reported certain somewhat similar irregularities in anther development in *Salix*.

MEGASPORES.—A complete series in the development of the ovule from the first protuberance was studied. The earliest stages show no differentiation of sporogenous tissue. The first difference to be noted is in ovules that are somewhat advanced; and these show only a difference in the size of the cells, there being no definite arrangement of these and no difference in staining reaction. Certain characteristic groups of these larger cells are shown in figs. 1, 2, and 3; the first two are from the same section. Often there are only two large cells, as may be seen in fig. 1, but in this case a third cell is below these two. Fig. 2 has four large cells that evidently were produced from one cell by two successive divisions, thus giving a rather striking resemblance to four megaspores; the wall between the two upper cells is very faint. At this stage, if the section is not perpendicular to the wall, one gets the impression of two nuclei without a separating wall, as CHODAT (**3**) has shown in his fig. 660; but I found no case in which the wall was really lacking. Fig. 3 is an ovule with one of the large cells in mitosis, showing the 20 chromosomes of the diploid generation. The ovule is somewhat larger before the difference in staining reaction appears, and the difference in the size of the cells is also more striking (fig. 4).

The inner integument begins to develop at this time. Fig. 5 has both integuments and the sporogenous cell is in synapsis. Synapsis was not found in younger ovules, but apparently it continues for some time, as it was often found in much older ovules, judging by the development of the integument. CHODAT'S fig. 660, *c* (**3**), is similar to fig. 5, except that he shows the nucleus without other contents than the nucleolus. Only a few instances were found in which more than one cell showed both by size and staining reaction the sporogenous characteristics. Fig. 6 gives two sporogenous cells, the cell with the nucleus in synapsis being much the larger. In fig. 7 the cells are approximately the same size, but the section was cut so that one cell was unfortunately directly over the other. Here the cell in synapsis is somewhat shorter and broader than the other. The walls of one cell are dotted in, but the walls of the other and both nuclei are drawn.

The mother cell divides in the usual manner (figs. 4, 8, 9). A full series was studied, but only a few drawings will be shown. In fig. 5 the synapsis stage is shown and in fig. 8 the spirem. The chromosomes are quite short and thick in fig. 9, and the haploid number (10) can be counted. The daughter cells sometimes differ slightly in size, but as a rule the difference is not marked (fig. 10). In fig. 11 the lower daughter cell has the spindle already formed for the second division, while the upper daughter cell has only formed the chromosomes, the nuclear membrane being still complete and very distinct. But in fig. 12 both daughter nuclei are in the early telophase of this division. In the upper cell one chromosome did not reach the pole and was left out of the megaspore nucleus. This condition was seen only a few times; and, as the upper megaspore always disintegrates in the material studied, it does not seem to be of any importance in the life-history of this plant. One example of the same condition was found in the first division. Here it might affect the life-history; for very often the second megaspore develops. If the nuclei continued to divide as usual, this might give an egg with one less than the usual number of chromosomes, in this case 9 instead of 10.

Figs. 13–15 show the different positions of the megaspores, a straight row in fig. 13, the two lower in a row and the two upper side by side in fig. 14, and approaching the tetrad form in fig. 15. CHODAT (**3**) gives in his fig. 661 a straight row of four megaspores and in fig. 662 a row of three cells; in both cases the lower megaspore has enlarged to produce the embryo sac.

EMBRYO SAC.—While in angiosperms it is probably true that the lowest of the four megaspores usually produces the embryo sac, the others disintegrating, cases showing that any of the four may function have been reported, and in some instances all four show sac tendencies. COULTER and CHAMBERLAIN (**4**, p. 84) give a summary of the literature on this subject. In *Parnassia* apparently the second or the third as frequently develops as the fourth (figs. 16–29), but no case was found in which the first developed. These figures show that often two of the megaspores begin to develop, apparently either two of the lower three, second and fourth (figs. 16–18), second and third (fig. 17), third and fourth (figs. 22 and 24). In fig. 25 one of the two upper adjacent megaspores and the fourth one began to develop, but the upper one is in the best condition, the fourth one being less dark than the other two, but darker than the upper one. The epidermis is quite pale over this spore. Fig. 23 has the appearance of five megaspores, but one nucleus is quite small with apparently only one chromosome, and is probably the result of an abnormal division like that shown in fig. 12.

The epidermal layer of the nucellus begins very early to disintegrate. These cells nowhere had the usual appearance of disintegrating cells. As is well known, cells disintegrating under apparently similar conditions stain deeply and have a more or less crushed or squeezed appearance. But here they seem to grow paler, as if the cytoplasm within them were diminishing, and finally all contents disappear. Later the walls also are more or less completely absorbed. An attempt to show this is made in figs. 24, 26, 27. In fig. 24 the whole epidermal layer is pale almost to the base of the fourth megaspore; in figs. 26 and 27 the cells are disappearing from the upper part of the nucellus, leaving the megaspores lying next to the inner integument. The disintegration in this region continues until only the lower end of the sac is inclosed by nucellar tissue, the greater part of it being in contact with the integument and having no cells between it and the micropyle (figs. 30, 31, 33–36). CHODAT'S (3) figs. 661–666 show this disintegration of nucellar tissue. He says:

> Chez beaucoup de Gamopétales et ches quelques Dialypétales la mégaspore qui s'est développée dans un très petit nucelle dissont le sommet de celui-ci et fait saillie an dehors dans le micropyle.

The disorganization of this layer of cells may furnish food to the upper megaspores and thus give them a better chance to develop than they would otherwise have. On the other hand, it is altogether possible that this disintegration is due to the unusual activity of these megaspores.

Fig. 27 shows a two-nucleate sac that developed from the second megaspore; the third megaspore is quite large and as yet shows no signs of disintegration. The fourth megaspore is fast disorganizing, being a darkly stained almost structureless mass. The first megaspore and the nucellar layer over the upper part of the sac show only traces of their former existence. An embryo sac developing from the fourth megaspore is shown in fig. 28. The nucleus is in mitosis for the first division, and the 10 chromosomes can be counted. The three upper megaspores are completely disorganized, and the nucellar cells near the micropyle are paler and with very little contents. The vacuole appears early in the two-nucleate sac (fig. 29). It is not common to find the second and the third megaspores persisting so long as they have here. The two upper nucellar cells have very little cytoplasm in them and stain much lighter than the others.

In fig. 30 an entire ovule at a little later stage is shown with less magnification. The nucellar layer has disappeared completely from around the upper part of the sac, leaving it in contact with the inner integument and an open micropyle all the way to the sac. The only part of the nucellus remaining is that below the lower nucleus of the two-nucleate sac. It is interesting to note that SHREVE (**20**) has shown a similar figure for *Sarracenia*, all the nucellar tissue except that at the base having been destroyed. The loose, spongy tissue is already appearing in the chalazal end of the ovules. This becomes very conspicuous in older stages.

Figs. 31 and 32 show the second mitosis in the embryo sac. In one nucleus of each sac it is possible to count the 10 chromosomes. In the first the chromosomes have been formed in both nuclei, in the second only in the lower one; the upper one has the spirem very thick and short and probably shows the early stages of segmentation. In both ovules the nucellar layer has disappeared from the upper half of the sac. The spindles for the second division are at right angles to each other (fig. 33). This sac developed from the second megaspore, and in this case the third one has also begun to develop. Fig. 34 shows a four-nucleate sac with the chromosomes more or less completely segmented for the third division. The nucellar layer has disappeared from the upper two-thirds of the sac. The inner layer of cells of the integument is shown on one side of the sac in fig. 35. The sac nuclei are in the late anaphase of the third division. The upper spindle is almost perpendicular to the paper, and so it is not easy to show it correctly. Each of these spindles shows the thickening of the spindle fibers in the center, characteristic of early wall formation, but further development of the walls does not take place, as is shown in fig. 36. The nucellar layer is represented by a more or less distinct line of stuff which can be traced to the perfect cells below the sac. The darker thicker mass near the micropyle is probably the remains of the megaspores.

The eight nuclei arrange themselves in the usual fashion (fig. 37). In this figure the egg lies just back of the synergids and only the lower part of it is shown in the drawing; and the polars are almost in contact. Here the large nucleoli characteristic of these nuclei are well shown, the nuclei having very little other stainable material in them. In this case practically all of this material is shown in the drawing, which was made not with a single focus, but by focusing in all parts of the nuclei. At any given focus one's first impression of the nucleus is an empty circle except for the very large nucleolus. The inner layer of cells of the integument is drawn on only one side of the sac. This layer has the appearance of the so-called tapetum or jacket layer formed in many of the Sympetalae, as well as in other forms, and is quite different in appearance from the adjacent cells. CHAMBERLAIN (**1**) has shown it in *Aster novae-angliae*. EICHINGER (**6**) says:

> Bei unserer *Parnassia* kann man füglich von einem Tapetum nicht sprechen, die innersten Zellen des Integuments unterscheiden sich nicht allzusehr von den andern.

But in my material the difference in shape and staining was striking.

Small vacuoles are already present in the synergids. One synergid shows the beginning of the indentation, *Leiste* of STRASBURGER (**21**), which in later stages gives a caplike appearance to the upper part of the synergid. It seems to be related to the cytoplasm of the sac, that is, it is always just where the cytoplasm of the sac reaches its highest point of contact with the synergid. It seems probable that, as the filiform apparatus develops (being of cellulose, it is somewhat stiff) and the synergids elongate, this upper stiffer part does not change shape so much as the lower part. A filiform apparatus is common in angiosperms, but it is not always so strikingly developed as here. In *Die Angiospermen und die Gymno-*

spermen (**22**), STRASBURGER shows (pl. 2, fig. 19) a filiform apparatus, but no notch in *Polygonum divaricatum*. COULTER and CHAMBERLAIN (**4**, p. 94) say that "such beak-like extensions of the sac and synergids are usually associated with narrow and long micropyles." But in *Parnassia* the micropyle is usually wide open and even all nucellar cells have disappeared from this region.

A similar filiform apparatus and notch are shown by STRASBURGER (**21**) in *Santalum*. This is shown quite clearly in spite of the very imperfect technique of that time. In *Santalum* the notch seems to be definitely related to the embryo sac wall, the upper part of the synergids protruding beyond the wall, and this indentation being just against the upper end of this broken wall. NAWASCHIN (**16**) shows in his fig. 9 a very deep notch in the synergids of *Helianthus annuus*. The synergids are pointed, but do not show the lines of the filiform apparatus in the upper part, although just below the notch the lines are quite distinct. This part of the figure is not described, and it may be that the upper part has the usual lines of the filiform apparatus, but they failed to appear in the plate. Here the notch seems definitely related to the cytoplasm of the sac, very much as it is in *Parnassia*. JUEL (**14**) shows the usual embryo sac in *Saxifraga granulata*, but does not describe a filiform apparatus. This stage he shows in a microphotograph which is quite indistinct in this region. Fig. 38 is slightly older; the filiform apparatus is beginning to develop in the synergids. The nucleus is above the vacuole in one and below it in the other synergid. Fig. 39 has an unusual development of the vacuoles in the synergids; here the polars are in contact. In fig. 40 the vacuoles are below the nuclei in both synergids, and the polars have fused, forming the primary endosperm nucleus. The filiform apparatus and notch are quite distinct by this time. Another view of a sac of about the same stage is shown in fig. 41. In this ovary many sacs were still in the four-nucleate condition.

The upper part of a mature sac is shown in fig. 42. The polars have already fused. In *Parnassia* they apparently always fuse immediately, as they are fused in all the mature sacs examined. The caplike filiform apparatus is always very conspicuous at this stage, and stains red with Congo red, which shows it to be cellulose. The inner row of cells of the integument next to this part of the sac is disintegrating, the disorganization being more or less complete as far down as the last cell drawn, which seems to be still active, as both nucleus and cytoplasm have the usual staining reaction and structure of active cells. Fig. 43 is the other view of a similar sac, being cut at right angles to that of fig. 42; the other synergid is directly under the one drawn. Here the egg apparatus is farther up in the micropyle, and a few of the cells of the integument over the filiform cap have entirely disappeared. CHODAT (**3**) shows an embryo sac before and after fusion of the polars in his figs. 664 and 665, but does not show the filiform apparatus of the synergids. His fig. 677 suggests the possibility of its presence, but does not show it clearly. The pollen tube is just below it.

In many ovules the egg apparatus is entirely in the micropyle, a few of the cells of the integument being disorganized in most instances (fig. 44). The whole egg apparatus has the appearance of being squeezed into a space too small for it. The polars have fused. In fig. 45 the synergids lie one above the other in the micropyle, the egg being just at its entrance. These synergids show the notch and the filiform appearance quite distinctly. If the synergids are not entirely separated, they may have somewhat the appearance of pollen tubes; but it is always easy to distinguish them from the latter by the difference in staining reaction, and by the fact that the real tube structure is lacking. A diagram with less magnification (fig. 46) shows the whole upper portion of the ovule. Fig. 47 shows one synergid nucleus just at the entrance of the micropyle, some of the cytoplasm of this synergid being entirely outside of the ovule. In fig. 48 the entire egg apparatus is just at the entrance to the micropyle, with the polars in contact in the upper part of the sac. A few ovules were seen in which the whole of the egg apparatus was entirely outside of the micropyle. These figures with the synergids in the micropyle are very similar to the structures shown by CHODAT (**3**) in his figs. 675–676, which he calls pollen tubes.

POLLEN.—The anthers present the usual four-lobed appearance, with four sporogenous regions. A group of mother cells in more or less perfect synapsis is shown in fig. 49. After synapsis there is a thick spirem which segments into 10 chromosomes (fig. 50). The telophase is shown in fig. 51. The chromosomes seem to remain distinct here (figs. 51 and 52) and could often be counted after the nuclear membrane was formed. Fig. 53 shows the metaphase of the homotypic division; the two spindles being almost at right angles, one nucleus is cut exactly at the plate and the other shows almost all of the spindle. The formation of the tetrad is shown in fig. 54. Different views of the microspores soon after their formation are shown in figs. 55 and 56. The nucleus divides at once to form the tube and generative nuclei (figs. 56–59). The wall apparently disappears early, as several gametophytes without a wall separating the two nuclei were found in these same anthers. The stages shown in figs. 55–59 come from the same anthers, all the anthers of this flower being in the same stage.

FERTILIZATION.—The pollen tube comes through the micropyle, which is usually open (figs. 30, 42, 43), curves around the tip of the synergid, and seems to empty into one of the synergids below the notch (fig. 60). In this sac the other synergid is quite dark, and the tube can be traced to this dark mass. Fertilization has already taken place, and there are two endosperm nuclei. In fig. 61 the same dark appearance of one synergid is found, and again the other synergid is unchanged. Fusion of the sex nuclei has already taken place; both the egg and the primary endosperm nucleus show much more chromatin than they do in the mature sac (fig. 43). Several pollen tubes were seen, all about the same stage. Only one more will be shown (fig. 62). In this the bending of the tube around the upper part of the synergid is not so clearly shown, as the section was not so fortunate in position as that in fig. 60, yet the tortuous course is quite evident. But especially clear is the emptying of the tube into one synergid. The contents of this synergid consist of a very darkly stained mass in which no structure can be distinguished except one nucleolus, which is quite clear because of its bright red color in the dark purplish mass. It is probably the nucleolus of the synergid nucleus. The other synergid is in the next section and is quite normal in every respect.

GUIGNARD (11) in *Nicotiana Tabacum* and *Datura laevis* reports the pollen tube passing into one synergid and discharging its contents there. JUEL (14) has described a similar passing of the contents of the pollen tube into one synergid in *Saxifraga granulata.* CHODAT (**3**, p. 552) says:

> Lorsque le noyau fécondant est entré dans le sac on remarque qu'au moins l'une des synergids perd sa turgescence et se désorganise.

In his fig. 677 he shows a pollen tube which from the drawing might be either inside or outside of the synergid. In this mass are three nuclei, one evidently the synergid nucleus. Fig. 63 shows a sperm cell in each synergid. There seems to be a distinct layer of fine-grained cytoplasm about each of these nuclei. One synergid also has another somewhat irregular mass of nuclear stuff which is probably the tube nucleus. This sac was cut slantingly, so that the micropyle and filiform apparatus were in another section, but no trace of the pollen tube was found in this region. Another ovule in the same section had an embryo of five cells. But only a very few embryos were present in this ovary, and the other ovules did not show evidence of fertilization; so that probably only a few pollen grains had reached the stigma. These two dark synergids, each containing a sperm cell, might be interpreted as evidence of two pollen tubes in the same sac. But as there is no other trace of pollen tubes or other nuclei, and the egg and primary endosperm nucleus do not have the appearance of having been fertilized, it seems best to suppose that only one pollen tube has entered and that it burst just where the two synergids are in contact. In this way it would be possible for part of the contents to pass into one synergid and part into the other. Both synergids are quite dark and show little trace of vacuoles, which are quite conspicuous in mature sacs.

NAWASCHIN (**16**) says that after the pollen tube passes the micropylar canal and the nucellus of the ovule, and its tip is in contact with the embryo sac, one of the synergids bursts and pours part of its contents into the micropyle. This forms a half-empty tube of this synergid, and the sudden diminution of pressure causes the pollen tube to burst and its contents are poured out next to this synergid into the sac. Then the sperm nuclei begin active movement toward the depression in the "Endospermanlage," and move from there to the female cells. In *Parnassia* it is very evident that the pollen tube passes around the tip of the synergid without either synergid or pollen tube bursting, and that the tube empties into the synergid just below the notch. This process itself was not seen, as unfortunately all my material was too old to show this, even fertilization having already taken place in every case except one. But the pollen tubes themselves were unusually clear; they could often be traced through the entire micropyle to the point where they entered the synergid. CHODAT (3) shows the sex nuclei in various stages of fusion in his figs. 678–680.

EMBRYO.—One and two-celled embryos showed nothing unusual. The endosperm nucleus usually divides first; only one exception to this was seen (fig. 65). Here there is a five-celled embryo with the endosperm nucleus still undivided and somewhat amoeboid in shape, which is also unusual in *Parnassia*. One sac was seen with a two-celled embryo and two endosperm nuclei, one near the embryo and the other near the antipodals, and one synergid still perfect. Empty pollen tubes are often very persistent in *Parnassia*. It is not uncommon to find a pollen tube that can be seen through the greater part of the micropyle and with the curve at the entrance to the sac where it passes around the beak of the synergid, but with little trace of the synergids below this, when the embryo has 20 or more cells. In the second division in the embryo, the upper cell again divides in the same plane as the first division, while the lower cell divides at right angles (fig. 64). Fig. 65 shows the five-celled embryo. Not many embryos of this stage were seen, but this seems to be the usual arrangement of cells. Fig. 66 gives the next stage, where the upper cell had again divided in the longitudinal direction. In fig. 67 the dermatogen is differentiated, and a layer of endosperm about two cells in thickness extends entirely around the sac next to the wall; in the center are a few free nuclei. Soon the plerome and periblem are also differentiated, as can be seen from the end of the embryo in fig. 68. This entire embryo is outlined in fig. 69 and the plerome is dotted in. The two cotyledons are already formed, and the embryo now completely fills the upper two-thirds of the sac, except for a layer of endosperm about two cells thick around it. The lower third of the sac is filled with endosperm. CHODAT (3) in his fig. 756 shows embryos from the two-celled stage to the differentiation of the dermatogen; his figures 756–775 are similar to my figures 75 and 81.

Saxifraga

Several species of *Saxifraga*, growing in the Botanical Garden in Bonn, were examined, to be sure that the usual form of this genus was known. The same methods of fixing and staining were used for *Saxifraga*, *Heuchera*, and *Drosera* as had been employed with *Parnassia*.

JUEL (**14**) has given a description of *Saxifraga granulata* which agrees in all the stages shown with the stages here figured; and I have examined *S. ligulata*, *S. sponhemica*, *S. cordifolia*, and *S. crassifolia*, which seem to be so similar that the same figures could be used for each. Not much work was done with the reduction division; but the reduced number of chromosomes in *S. sponhemica* is about 15. JUEL (**14**) found this to be about 30 in *S. granulata.* These two numbers are rather suggestive, especially since GATES'S (**10**) investigation of *Oenothera gigas* and STRASBURGER'S (**23**) discussion of this question.

Nothing unusual was seen in the pollen development of *Saxifraga*. The pollen grains are small and with smooth, rather thin walls. It might be of interest to note that in many of the flowers of *S. cordifolia* some of the anthers contained pollen at least twice the usual diameter, and in some cases as much as four times. In one flower this large pollen was found in every other anther, the younger set of stamens all being affected. But not all flowers produced this large pollen, and it was usually irregular in occurrence when present. As all the later flowers were blighted, turning black before the inflorescence was out of the bud, this peculiarity of the pollen was probably due to a fungus; but this was not investigated.

Two young ovules of *S. sponhemica* from the same ovary are shown. Fig. 71 shows the archesporial cell, and fig. 72 a later stage in which there is one sporogenous cell and the primary parietal cell has divided. The mother cell stage is shown in fig. 73, with two parietal cells. In fig. 74 there are three sporogenous cells, only one of which has reached the mother cell stage; a later stage is shown in fig. 75. There are three parietal cells above the mother cell in fig. 76. The whole of this ovule is shown in fig. 79. In *Saxifraga*, so far as examined, the megaspores are always in a row (fig. 78), and the fourth one develops the embryo sac. Not so much material was examined as in *Parnassia*, but enough to be sure that the development of the other megaspores, if it takes place at all, is not common. The position of the megaspores in the nucellus is shown in fig. 79. Their great depth in the nucellar tissue is in striking contrast to *Parnassia*, where they are immediately below the epidermis, which is disorganizing at this stage.

Fig. 80 outlines an entire ovule with a two-nucleate embryo sac. There are no air spaces, the whole ovule being very compact and much more massive than that of *Parnassia*. The egg apparatus of a mature sac is shown in fig. 81. The synergids have a well developed filiform apparatus and a notch almost if not quite as deep as that in *Parnassia*. A diagram of this entire sac is shown in fig. 82. Two of the antipodals had disappeared. The polars have already fused and the primary endosperm nucleus is near the base of the sac. This seems to be its usual position in *Saxifraga*, at least in the examples I studied. JUEL (**14**) shows it near the middle or toward the antipodal region in *S. granulata* at fertilization. Fig. 83 is a young embryo which has just been differentiated into long suspensor and embryo proper. Two endosperm nuclei are shown.

Heuchera brixoides

This species corresponds so closely with *Saxifraga* that only three figures will be shown. There is usually one mother cell in *Heuchera*. One ovule with two mother cells (fig. 84) is shown, a later stage (fig. 85) with a large amount of parietal tissue, and a mature embryo sac (fig. 86). The placentae of *Heuchera* are like those of *Parnassia*, and quite unlike those of *Saxifraga*.

Drosera rotundifolia

This material was collected near Bonn. ROSENBERG (**19**) has worked out a very interesting chromosome relationship of *D. rotundifolia*, *D. longifolia*, and *D. intermedia*. In his early paper (**18**) he does not figure certain stages which I need for comparison, only quoting from C. A. PETERS (**17**, p. 275):

> Each nucellus produces a sporogenous layer of four cells, but no tapetum. Three cells of the sporogenous tissue soon disintegrate, leaving the fourth, which is the mother cell of the embryo sac and which undergoes subsequent cell division as is usual in angiosperms.

I shall give a few figures, therefore, in order to compare them with *Parnassia* and *Saxifraga.*

The mother cell in synapsis is shown in fig. 87. It will be seen that like *Parnassia* and *Saxifraga* no parietal cells were produced by the archesporium. This is the commonest condition in *Drosera.* But frequently a parietal cell is cut off which divides, as is shown in fig. 88, giving a row of two parietal cells above the mother cell. Occasionally more than one sporogenous cell is produced (fig. 89); but I saw no evidence that more than one embryo sac was produced, or even that more than one cell reached the mother cell stage. The usual row of four megaspores resulting from these two positions of the mother cell are shown in figs. 90 and 91. In some instances the megaspores are not in a row, as ROSENBERG (**19**) has shown in his text fig. 27, *B*, which is similar to fig. 25 in *Parnassia.* So far as examined, only the fourth megaspore develops in *Drosera.* Not so much material was cut as for *Parnassia*, but it is at least certain that the development of the other spores is not common as it is in *Parnassia.*

In *Drosera*, even in the mother cell stage (fig. 87), air spaces begin to develop in the chalazal region of the ovule. These spaces are quite large by the time the embryo sac has reached the two-nucleate stage (fig. 92), and in the mature ovule they are at least as strikingly developed as in *Parnassia.* The embryo sac occupies only the upper third of the nucellus even at maturity, quite in contrast to *Parnassia* and *Saxifraga.* The nucellus also begins to show its peculiar enlargement of cells. The outer layer of nucellar cells, except those directly over the embryo sac, increase enormously in size without increase of cytoplasm or size of nucleus; the latter lies next to the inner side of the cell. This enlargement of the nucellar cells, as well as the air spaces, reduces the specific gravity of the seed. DIELS (**5**) says:

> They are by their constitution capable of floating. HOLZNER states that the seeds of *D. rotundifolia* at a temperature of about 20° are capable of floating for about a month.

In fig. 93 the third division in the sac is shown and enough of the nucellus to show the differentiation in it. In one nucleus the 10 chromosomes may be counted.

The mature sac (fig. 94) has the usual appearance. The synergids have a well developed filiform apparatus and notch. The former is somewhat more dome-shaped than in *Parnassia*, where it is pointed. The synergids are also rather long, reaching almost as far as the lower edge of the egg. The polar nuclei have already fused. Fertilization apparently takes place as in *Parnassia*. The pollen tube passes around the filiform apparatus and seems to enter one synergid (fig. 95). Here probably the fusion of the sex nuclei has already taken place, as only one nucleus can be distinguished in the lower part of the dark synergid and probably another in the still darker mass higher up. Fig. 96 is clearer in this respect. A small bit of the pollen tube can be seen in contact with the filiform apparatus. This synergid is somewhat darkly stained, but still all structures are distinct, the notch and two nuclei; these are the synergid nucleus and the tube nucleus from the pollen tube. The other synergid is very pale and all the lower part has disappeared. The fertilized egg has not yet divided, but the primary endosperm nucleus is in mitosis; the spindle fibers are forming. So far as examined, this nucleus always divides before the fertilized egg in *Drosera*. Many cases were seen with two endosperm nuclei and the egg still undivided.

Discussion

Three other genera of the Saxifragaceae have been more or less completely worked out. EICHINGER (7) figures an ovule of *Chrysosplenium* with mature embryo sac that has three layers of nucellar tissue above the sac. In *Astilbe* WEBB (25) reports several archesporial cells and one or even two or three megaspore mother cells beginning to divide. The embryo sac is deep in the nucellar tissue, but no filiform apparatus is shown. The embryo has a suspensor of several cells. FISCHER (9) in *Ribes aureum* shows ovule development similar to that of *Saxifraga*, except that the filiform apparatus is not shown. TISCHLER (24) in a mature embryo sac of *Ribes sangunineum* shows pointed synergids but no filiform apparatus or notch. These cases may indicate that these three genera do not have the filiform apparatus and notch. But it is also possible that the material studied was not at the right age to show these best, or was not cut to the best advantage for these particular structures.

In a recent number of *Das Pflanzenreich* on Droseraceae, DIELS (**5**) says, in discussing relationships:

> Die mehrfach den Droseraceen angeschlossene Gattung *Parnassia* wird neuerdings nach dem Vorgang von ADAMSON, ENDLICHER, LINDLEY, und PAYER, allgemein ausgeschlossen nachdem DRUDE in seine gründlichen Eröterung der Frage (Linnaea **39**:293. 1875) auf die gewichtigen Bedenken practischer Natur' hingewiesen hatte, die einer Überführung von *Parnassia* zu den Droseraceen im Wege stehen.

ENGLER (**8**), in a note in connection with the Sarraceniaceae, concludes with these words:

> Die Droseraceae nähere sich dadurch in diagrammatische Beziehung manchen Saxifragaceae, von denen *Parnassia* auch allgemein den Droseraceae zugerechnet wurde.

The following is a rather free translation of EICHINGER'S (**6**) summary of the characters which differentiate *Parnassia* from Droseraceae:

1. *Germination.—Parnassia* shows normal germination; cotyledons do not function as an absorbing apparatus. The Droseraceae have no primary root; cotyledons have more or less the function of an absorbing apparatus.
2. *Leaf structure.*—The nervature is different. *Parnassia* possesses a typical leaf structure, in the epidermis tannin; the Droseraceae have no typical assimilation tissue and often chlorophyll in the epidermis, and always more or less modified glands.
3. *Flowers.*—All species of *Parnassia* have staminodia; the Droseraceae have not.
4. *Befruchtungsvorgang* (apparently pollination).—It is apparently similar in species of *Parnassia*, has no analogy to the Droseraceae, but has to *Saxifraga.*
5. *Androecium.—Parnassia* possesses small simple pollen grains; all of the Droseraceae have tetrads.
6. *Gynaecium.—Parnassia* has stalked placentae, a very striking conductive tissue, the nucellus is small-celled and soon vanishes, the embryo is well formed and fills the almost endospermless seed. *Drosera* at least has flat placentae without conductive tissue, characteristically differentiated nucellus, and all of the Droseraceae have small, round, imperfect embryos and much endosperm.

HALLIER (**12**) says:

> Under the Saxifragaceae the genus *Parnassia* takes an isolated place. According to its peculiar habit, its low rosette of long-petioled oval leaves, its one-flowered, long, almost leafless flower-stalk, and the lack of hairs, it evidently belongs not to the Saxifragaceae, but in ENGLER'S order Sarraceniales, which, through the frequent appearance of oval, long-petioled, fleshy leaf blades,

long, one or few-flowered peduncle, fleshy, white, oval floral leaves, and its great predilection for wet or moist places, reveals its descent from the relatives of the Nymphaeaceae, and it manifestly has nothing to do with the Saxifragaceae, which are nearly related to the Rosaceae. Apart from the peculiar staminodia, which are evidently morphologically equivalent to the staminodia of many Nymphaeaceae, the fibers (*Fäden*) in the *Rafflesia*, flower, and the corona of *Passiflora*, *Parnassia* fits closely to *Drosera* through its leaf-rosette, its long, almost leafless shaft, the calyx, the five beautiful white petals, the sessile stigmas, the numerous parietal ovules, the method of capsule opening, the small oblong seed, rich in endosperm, and moist habitat. Through its four-leaved (four-carpellate) seed coat it approaches *Nepenthes* also.

A summary of the parts studied by way of comparison may be helpful.

1. The ovule of *Parnassia* and *Drosera* are of the same shape, and both have large air spaces developed. That of *Saxifraga* is very compact and much thicker, and with thicker integuments.

2. In *Parnassia* the archesporium of the ovules is hypodermal and forms no new cells above it. *Drosera* usually develops in the same way, but sometimes there is a single layer of cells between the mother cell and the epidermis. All the Saxifragaceae studied form the archesporium in the same way, but by the time the mother cell stage is reached there are several layers of cells above it.

3. In *Parnassia* the embryo sac comes to lie next to the integument except the very basal portion, all the nucellar cells above and at the side having been destroyed. In *Drosera* the nucellar cells above the sac have a squeezed appearance and are occasionally destroyed completely. At the side and below the sac the layer of cells next the epidermis enlarge very greatly, giving the nucellus of *Drosera* a very peculiar appearance. This may be only another means of decreasing the specific gravity of the seed. The sac of the Saxifragaceae has several layers of nucellar cells above it.

4. All three genera have an enormous development of the filiform apparatus of the synergids, and the notch is also strikingly developed. The filiform apparatus is pointed in *Parnassia* and Saxifragaceae, and less pointed or more dome-shaped in *Drosera*.

5. The primary endosperm nucleus in *Parnassia* and in *Drosera* is immediately below the egg. In *Saxifraga* it is almost in contact with the antipodals, and in *Heuchera* it is far below the egg.

6. The haploid chromosome number in *Parnassia* and in *Drosera rotundifolia* is 10, in *Saxifraga sponhemica* about 15, and in *S. granulata* about 30.

7. In *Parnassia* and *S. granulata* the pollen tube empties into one synergid, and apparently the same is true in *Drosera*.

With reference to the systematic position, EICHINGER (**6**) says that the joining of *Parnassia* to the Droseraceae would completely destroy the unity of this family. Its principal characteristic would be lost. The failure of a primary root, the defective differentiation of the assimilation tissue, the stipular structures, which recall the intra-ovarian scales of many water plants, the numerous secretion glands, the common appearance of cleistogamous and autogamous flowers, the high capability for regeneration, and the appearance of vegetative buds are most important. In *Parnassia* no such relation to water plants is found. If one looks for a suitable place in the system for *Parnassia*, one must admit that it had better remain with the Saxifragaceae. This family has at present so little unity that *Parnassia* makes no break in its systematic characteristics. In discussing the same question, HALLIER (**13**) says: according to the pronounced monocotyledonous type of venation of the sepals and petals, it seems to me to stand not very far from the point of departure of the monocotyledons and as the representative of a separate family, the Parnassiaceae, to belong near the Ranunculaceae, Nymphaeaceae, Droseraceae, and Sarraceniaceae. From the Saxifragaceae, in which ENGLER (**18**) has placed it, it is differentiated by the harp-shaped branching of the veins in the sepals, the large, long *Podophyllum* and *Sarracenia*-like anthers, and the ovule, which has a slender nucellus, as in other relatives of the Saxifragaceae.

After working over my material, I am of the opinion that *Parnassia* is much more closely related to the Droseraceae than to the Saxifragaceae, and that it should at least be put in the same order with the Droseraceae. For as shown above, *Drosera* and *Parnassia* are quite alike in their ovules and in embryo sac development, except as to the nucellus, in which neither is like *Saxifraga*. They differ also in that *Parnassia* has stalked placentae, while *Drosera* has not. *Drosera* has pollen grains in tetrads and *Parnassia* has them separate. But in neither of these characters does *Parnassia* agree with *Saxifraga,* whose placentae are still more dissimilar and whose pollen grains are perfectly smooth.

BAYLOR UNIVERSITY
WACO, TEXAS

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EXPLANATION OF PLATES XIV–XVII

All figures except the diagram in fig. 70 were drawn with the aid of the camera lucida; Spencer ocular no. 4 and 4 mm. objective were used for figs. 5, 30, 45, 46, 47, 48, 67, 68, 77, 79, 80, and 92; ocular no. 4 and 16 mm. objective were used for fig. 69; all others were drawn with ocular no. 4, 1.5 mm. (oil) objective.

The abbreviations used are as follows: *e*, egg; *m*, megaspore; ♂, male nucleus; *p*, pollen tube; *s*, synergid; *t*, tube nucleus.

Parnassia palustris

Fig. 1.—Young ovule with three large hypodermal cells; two shown in the drawing; the third is just back of these two.

Fig. 2.—A somewhat older ovule with four large cells in a row, evidently derived from a single hypodermal cell by two successive divisions.

Fig. 3.—A different arrangement of the large group of cells, one cell in mitosis, showing 20 chromosomes; from the same ovary as fig. 5.

Fig. 4.—Sporogenous cell differentiated as shown by size and stain; the inner integument is beginning to develop.

Fig. 5.—Synapsis and beginning of outer integument.

Fig. 6.—Two sporogenous cells; the larger one already in synapsis.

Fig. 7.—Two sporogenous cells of approximately the same size; the two cells were in the same section, one lying above the other; the larger cell has the nucleus in synapsis, the other one in an earlier stage.

Fig. 8.—After recovering from synapsis; spirem still very long.

Fig. 9.—Ten short chromosomes; the double character can be clearly seen in several.

Fig. 10.—The two daughter cells with chromosomes formed for the second division.

Fig. 11.—The micropylar daughter cell in same stage as fig. 10; the chalazal daughter cell has nucleus with spindle.

Fig. 12.—Both daughter cells in the telophase stage; in the micropylar cell one chromosome failed to reach the pole and so is omitted from the megaspore nucleus.

FIG. 13.—Four megaspores, apparently all increased in size but the first disintegrating, and the second and fourth larger than the third.

FIG. 14.—A different arrangement of the four megaspores, probably occurring more often than that shown in fig. 13.

FIG. 15.—Approaches still more nearly the usual tetrad arrangement.

FIGS. 16–22.—The variations in the early stages of the megaspores.

FIG. 23.—Apparently five megaspores; one nucleus is very small and seems to have only one chromosome, probably resulting from an abnormal division like that in fig. 12.

FIG. 24.—Third and fourth megaspores developing; the nucellar cells surrounding these are already showing signs of disintegration, and only the three at the base are still normal in appearance.

FIG. 25.—In this case also the epidermal cells are becoming pale, especially over the upper vigorous megaspore, which appears to be more active than the fourth.

FIG. 26.—The third megaspore forming the embryo sac and in mitosis for the first division; the epidermal layer partly disorganized, leaving the sac in contact with the inner integument and an open micropyle.

FIG. 27.—Two-celled sac formed from second megaspore; the third megaspore also developing; the epidermal layer still further disorganized.

FIG. 28.—Embryo sac formed from the fourth megaspore; first division showing 10 chromosomes, the other megaspores represented by a formless mass above; epidermal layer still perfect; integuments well advanced.

FIG. 29.—All the epidermal layer, especially the two upper cells of the nucellus, lighter than the adjacent integument cells; two-celled sac from the fourth megaspore; the second and third megaspores have persisted longer than usual.

FIG. 30.—The entire ovule with two-celled embryo sac; ovule with loose spongy tissue at base; nucellus entirely lacking over greater part of sac.

FIG. 31.—Two-celled sac with nuclei in mitosis for the second division; the 10 chromosomes may be seen in the upper nucleus; the upper half of the sac is in contact with the integument, the nucellus having entirely disappeared from this region.

FIG. 32.—Similar to fig. 31, but the lower nucleus somewhat in advance of the upper; in the lower the chromosomes are short and thick, while in the upper the spirem is segmenting.

FIG. 33.—Spindles for the second mitosis in the embryo sac; this sac developed from the second megaspore; the third megaspore also developing.

FIG. 34.—The four-nucleate embryo sac with the spirems more or less completely segmented for the third division.

FIG. 35.—Spindles for the third division in the embryo sac; in the upper part of the sac one spindle is almost at right angles to the paper.

FIG. 36.—Eight-nucleate sac soon after the third division.

FIG. 37.—Embryo sac soon after the organization of the egg apparatus, the egg being just under the synergids; only the lower part of it with part of its nucleus can be seen; polars not yet in contact.

FIG. 38.—Upper end of sac, slightly older than in preceding figure; one synergid has vacuoles above the nucleus, the other has them below it; the so-called filiform apparatus beginning to be differentiated near the tip of the synergids.

FIG. 39.—From older sac; the synergids have unusually large vacuoles, both above the nuclei; polars are in contact.

FIG. 40.—The polar nuclei have fused; vacuoles below the nuclei in the synergids; the filiform apparatus well developed and forming a caplike structure.

FIG. 41.—This sac was cut at right angles to the one above, showing the whole of the egg, but only one synergid; this ovary still contained four-celled sacs.

FIG. 42.—Upper end of mature embryo sac; the unusual development of the filiform apparatus clearly shown; the inner layer of cells of the integument disintegrating.

FIG. 43.—Same stage as the preceding, but with the egg apparatus still farther up in the micropylar region; some of the cells of the integument entirely disorganized.

FIG. 44.—The entire egg apparatus in the micropyle, the adjacent cells of the integument having disappeared and the egg apparatus having a squeezed appearance.

FIG. 45.—The upper part of an ovule outlined; the egg apparatus in the micropyle, one synergid lying above the other.

FIG. 46.—Egg apparatus in the micropyle, but the synergids so pressed together that it is not possible to differentiate them.

FIG. 47.—A diagram of the upper part of an ovule; one synergid has the upper end entirely out of the ovule, its lower end overlapping slightly the upper part of the other synergid.

FIG. 48.—The entire egg apparatus just at the entrance of the micropyle, giving the appearance of a pollen tube; the polar nuclei are in contact but have not yet fused.

FIG. 49.—A few pollen mother cells; in two of these synapsis is perfect, in the others almost so.

FIG. 50.—The 10 chromosomes may be counted in this pollen mother cell.

FIG. 51.—Telophase of the first division.

FIG. 52.—Telophase of the first division in which the 10 chromosomes are still distinct.

FIG. 53.—Metaphase of the second division, one nucleus showing the spindle and the other being cut parallel with the nuclear plate and showing the 10 chromosomes.

FIG. 54.—The tetrad with a few spindle fibers still present.

FIGS. 55–59.—Stages in the division of the pollen grain into vegetative and generative cells; in fig. 57 the 10 chromosomes are shown.

FIG. 60.—Fertilization: the pollen tube curved around the upper part of the synergid, which is quite dark; apparently the sperm has already fused with the egg; the endosperm of this sac is two-nucleate.

FIG. 61.—The male nuclei have already fused with the egg and the primary endosperm nucleus; the dark mass underneath the synergid and outlined through it is the other synergid and some material from the pollen tube.

FIG. 62.—Pollen tube entering one synergid; the other synergid is just back of this one; fertilization has already taken place; the endosperm nucleus has divided, the other endosperm nucleus being near the antipodals.

FIG. 63.—The upper end of an embryo sac; in each synergid is a synergid nucleus and another smaller dense nucleus (a male nucleus with fine-grained cytoplasm around it); one synergid has a third nuclear mass, the tube nucleus.

FIG. 64.—Mitosis in both nuclei of a two-celled embryo.

FIG. 65.—Five-celled embryo with endosperm nucleus still undivided.

FIG. 66.—An older embryo with traces of a synergid and showing one endosperm nucleus.

FIG. 67.—Older embryo with dermatogen layer differentiated; the endosperm forms a layer about two cells in thickness all around the sac with a few free nuclei in the interior, especially around the lower end of the embryo.

FIG. 68.—The basal part of older embryo, showing dermatogen, plerome, and periblem.

FIG. 69.—The same embryo outlined; a typical straight dicotyledonous embryo which fills about two-thirds of the sac except for the layer of endosperm about two cells in thickness; the other third of the sac is filled with endosperm.

FIG. 70.—A diagram of an abnormal flower; one anther has developed on a staminodium, two are normal, the others, more or less imperfect, are on the carpels, which are not so completely united as usual.

Saxifraga

FIG. 71.—*S. sponhemica:* outer half of young ovule showing archesporial cell.

FIG. 72.—Same: the archesporial cell has divided.

FIG. 73.—*S. crassifolia:* one mother cell.

FIG. 74.—Same: one mother cell, but two other cells are quite large and stain like sporogenous cells.

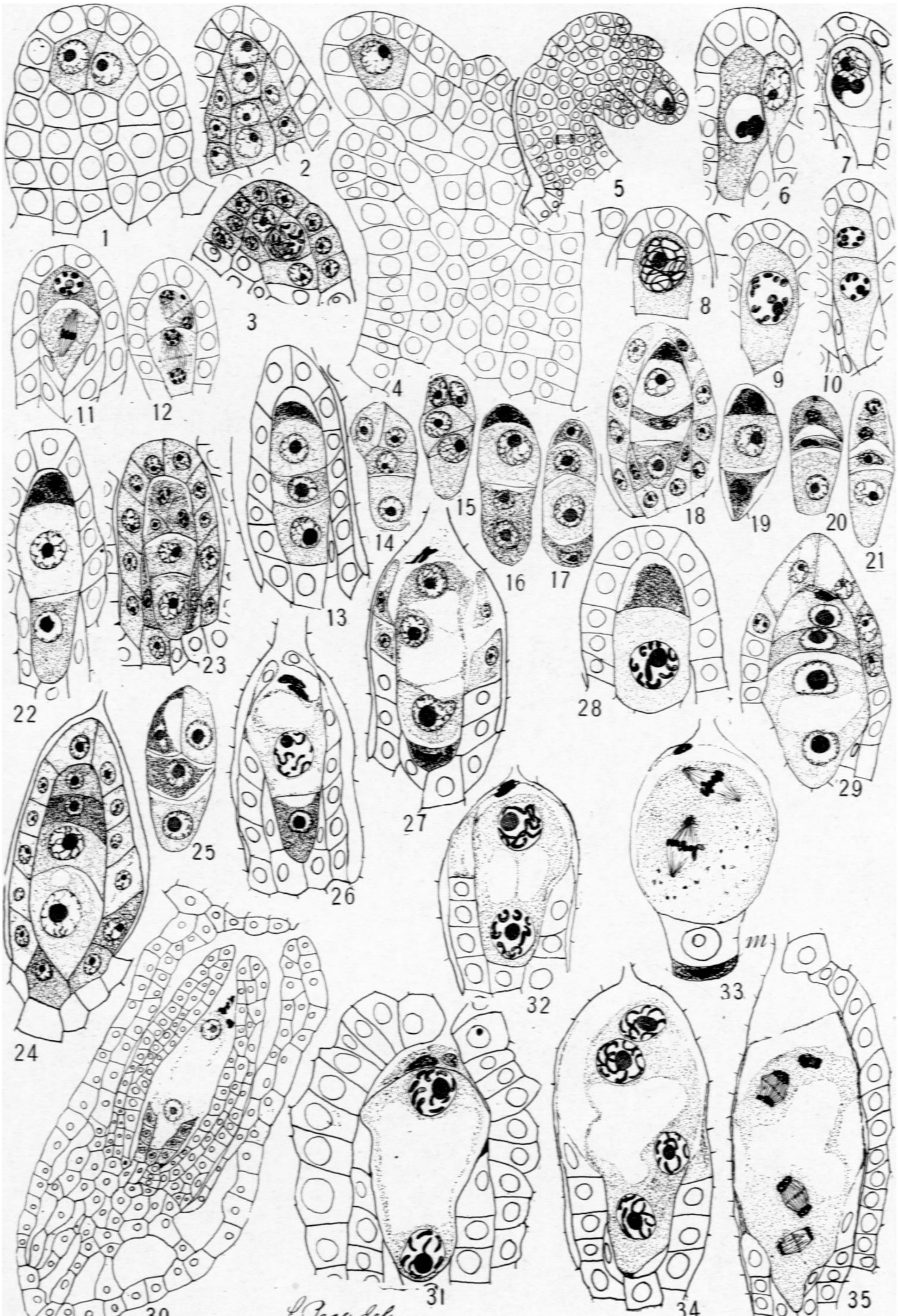
FIG. 75.—*S. cordifolia:* one sporogenous cell.

FIG. 76.—*S. crassifolia:* mother cell with three parietal cells.

FIG. 77.—Same: entire ovule with less magnification.

FIG. 78.—*S. ligulata:* megaspores; the lower are enlarging for the embryo sac.

FIG. 79.—Same: some megaspores showing nucellar tissue above.



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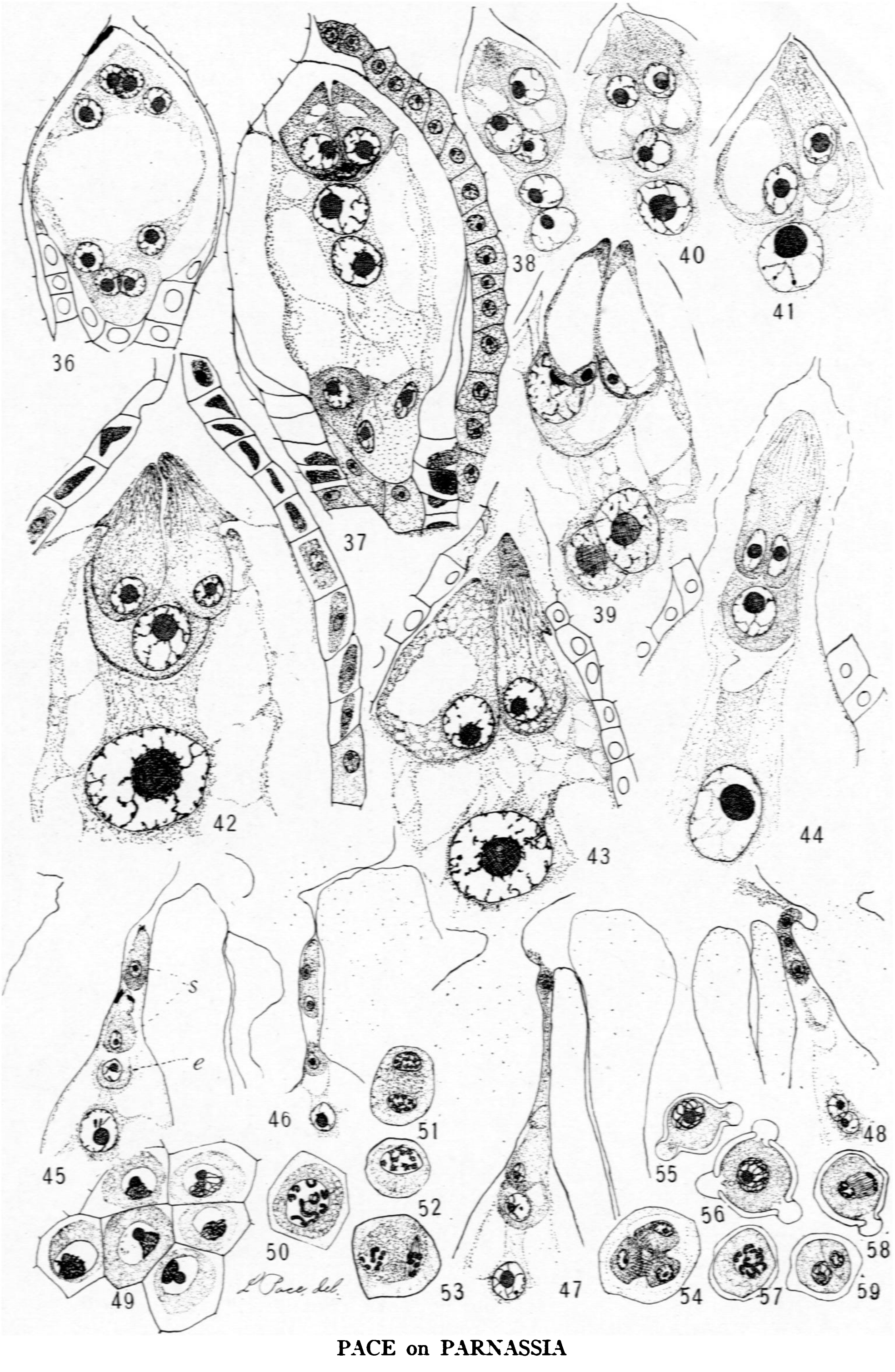

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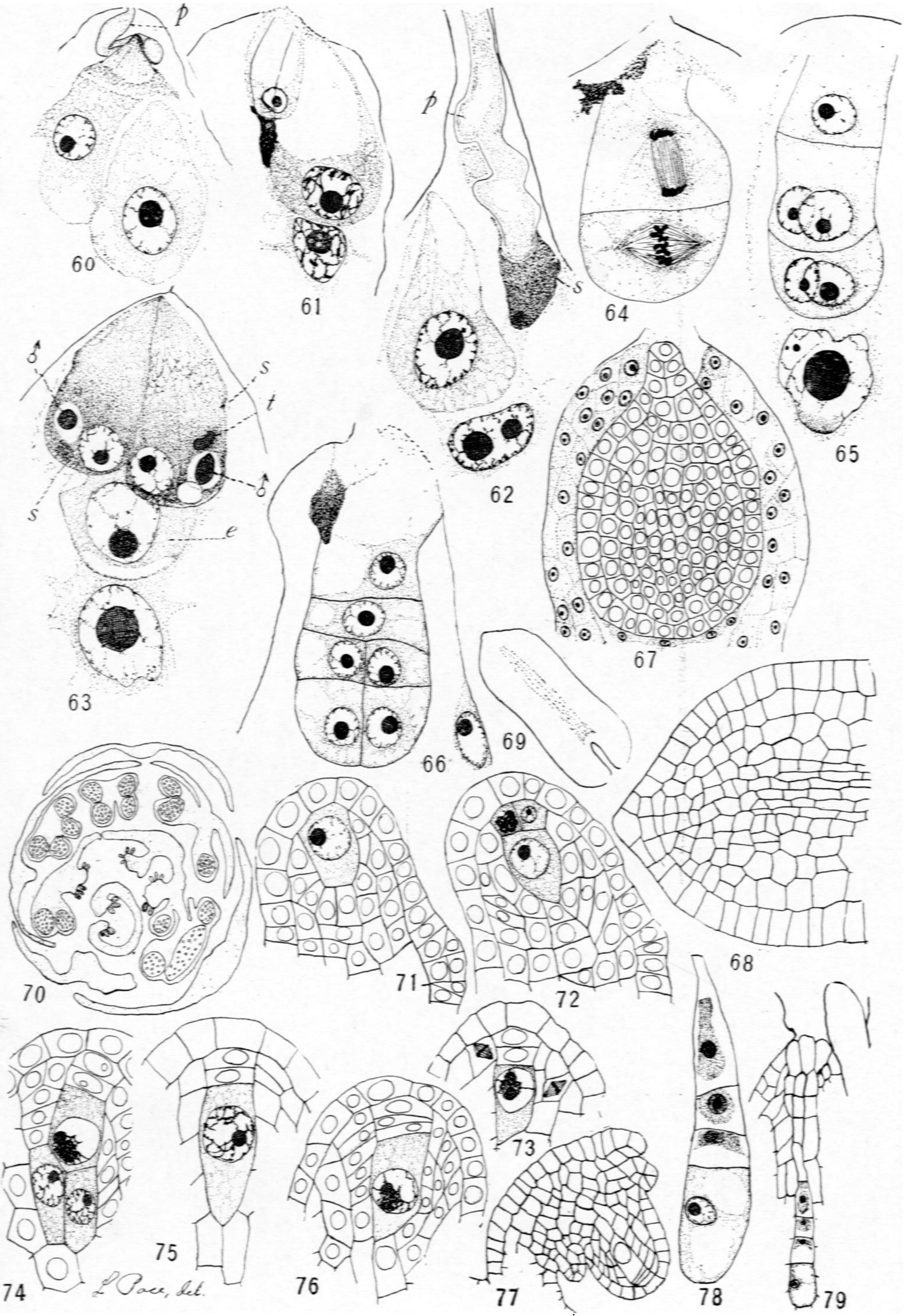

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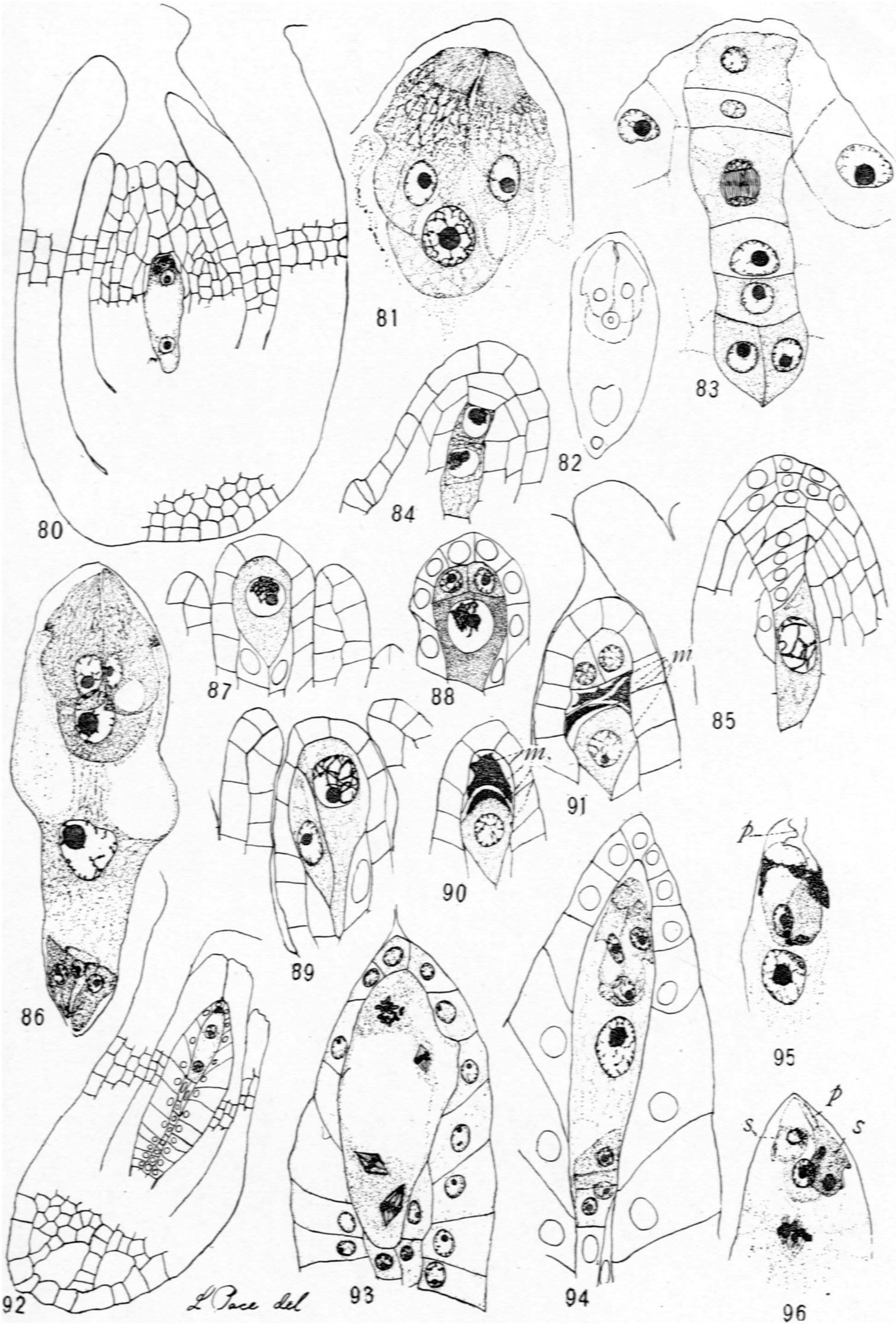

PACE on PARNASSIA

FIG. 80.—Same: a diagram of an entire ovule with two-nucleate sac; very compact tissue throughout the entire ovule.

FIG. 81.—*S. cordifolia:* egg apparatus.

FIG. 82.—Diagram of the same sac, showing one antipodal and the polars already fused near the base of the sac.

FIG. 83.—*S. crassifolia:* embryo and two endosperm nuclei.

Heuchera brixoides

FIG. 84.—Part of ovule showing two mother cells which are not exactly parallel and overlap slightly.

FIG. 85.—Mother cell after synapsis and deep in nucellar tissue.

FIG. 86.—Mature embryo sac; filiform apparatus and notch well developed in the synergids.

Drosera rotundifolia

FIG. 87.—Mother cell.

FIG. 88.—Mother cell with two hypodermal cells above.

FIG. 89.—At least two sporogenous cells, one of which has passed the synapsis stage.

FIG. 90.—Megaspores developed from a mother cell like that in fig. 87; the fourth megaspore has begun to develop the embryo sac, the other three are almost completely disorganized.

FIG. 91.—Similar megaspores, but developed from a mother cell like that in fig. 88.

FIG. 92.—An ovule with two-nucleate embryo sac; large air spaces and much spongy tissue in the lower part of the ovule; nucellar tissue with very small cells in center and very large ones next to the integument except just over the sac.

FIG. 93.—The third division in the embryo sac; in the upper nucleus the 10 chromosomes may be counted; the small nucellar cells just over the sac and the very large ones toward the base and the small ones in the center of the nucellus below the sac give the *Drosera* nucellus a very unusual appearance.

FIG. 94.—Mature embryo sac; the synergids have a well developed notch and a somewhat dome-shaped filiform apparatus; the polars have already fused.

FIG. 95.—An embryo sac with pollen tube passing around the filiform apparatus and apparently emptying into the synergid; probably the sex nuclei have already fused, but the mass is so indistinct one cannot be sure of the contents of the synergid region.

FIG. 96.—One synergid shows still a trace of the nucleus and the filiform apparatus; the other synergid shows the notch and above a bit of the pollen tube; in the lower part are two nuclei, probably the synergid nucleus and tube nucleus; the sex nuclei have fused and the endosperm nucleus is in mitosis.